

Integrative taxonomy of a new species of a bumble bee-mimicking brood parasitic bee, *Tetralonioidella mimetica* (Hymenoptera, Apoidea, Apidae), investigated through phylogenomics

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Abstract

A new species of bumble bee-mimicking brood parasitic bee, *Tetralonioidella mimetica* Orr & Zhu, **sp. nov.**, is described from China. The systematic placement of this species was initially challenging but was resolved using a combination of phylogenomic and COI barcode analyses, which strongly support the new species as a member of the genus *Tetralonioidella* Strand. Interestingly, the new species mimics the color pattern of both a bumble bee (*Bombus* Latreille), and its host *Habropoda* Smith species, a mimicry format previously unknown for bees. A review of the other *Tetralonioidella* species revealed three additional bee mimics, including two further likely model-host-brood parasite mimicry complexes. To

our knowledge, these represent the first documented three-tiered mimetic systems in bees. Several additional taxonomic actions recently became necessary in these and related taxa: *Tetralonioidella meghalensis* Dohling & Dey, 2024 is synonymized **syn. nov.** with *Habropoda radoszkowskii* (Dalla Torre, 1896) and *Varthemapistra* Engel, **stat. rev.** is again synonymized with *Habrophorula* Lieftinck. Our results also highlight issues with the generic classification of the tribe Melectini as currently used, as *Melecta* Latreille was found paraphyletic in relation to the remaining melectine genera. As a first step toward resolving this issue, we return the *Melecta* subgenus *Eupavlovskia* Popov, **stat. rev.** to genus level and discuss the ongoing systematic uncertainties regarding melectine taxonomy.

Keywords

Anthophila, brood parasite, Melectini, mimicry, Nomadinae, taxonomy

Introduction

The inner workings of mimicry have long fascinated scientists, but relatively few systems have been studied in detail in insects. Special focus has targeted Lepidoptera such as the genus *Heliconius* Kluk, 1780 and its relatives (Dasmahapatra et al. 2012; Kronforst and Papa 2015). Similarly in bees, work has predominantly focused on the bumble bees (*Bombus* Latreille, 1802) (Williams 2007; Ezray et al. 2019; Chatelain et al. 2023). However, much remains unstudied even in those better-known systems, and the genomic underpinnings of the complex color polymorphisms of this group are only now beginning to be understood (Owen and Plowright 1980; Williams 2007, 2008; Pimsler et al. 2017; Tian et al. 2019). Solitary bees are understudied in comparison, typically with mimetic relationships merely suggested but not definitively demonstrated (Blaimer et al. 2018; Bossert et al. 2020), such that many additional examples are expected across the bee tree of life (Chatelain et al. 2023).

The tribe Melectini contains >200 species of obligately brood parasitic bees worldwide, with especially high species and generic diversity in Asia (Ascher and Pickering 2023) where bumble bees also attain their peak richness (Williams 1998). There has been relatively little recent taxonomic research focused on this group compared to the second half of the 20th century (e.g., the works of Lieftinck), although Griswold and Parker (1999) and Onuferko et al. (2021) both provided valuable insights into their systematics. This group is dominated by the large genera *Thyreus* Panzer, 1806 (around 112 valid species) and *Melecta* Latreille, 1802 (around 55 valid species). The third largest genus, *Tetralonioidella* Strand, 1914, currently includes 19 species and has been repeatedly suggested to be the sister group to the remaining Melectini (Dubitzky 2007; Michener 2007; Niu et al. 2017; Sless et al. 2022). Far more restricted in its distribution than the near-Holarctic *Melecta* and the Eastern Hemisphere *Thyreus*, *Tetralonioidella* is known primarily from Eastern Asia, ranging from north China southward to Indonesia and from India into easternmost China.

Interestingly, the distribution of *Tetralonioidella* is concordant with the Asian-Oceanic hotspot of *Habropoda* Smith, 1854 species richness, and also corresponds closely to the range of *Elaphropoda* Lieftinck, 1966, which together encompass the known hosts of these brood parasites (Lieftinck 1972; Wu 2000; Michener 2007). Based pri-

Table 1. Suggested host associations of *Tetralonioidella* (= *T.*). *Elaphropoda* = *E.*, *Habropoda* = *H.*. Note that one species may use multiple hosts as seen in other Melectini (Lieftinck 1972).

Host	Host author	Parasite	Parasite author	Evidence	Source
<i>H. sutepensis</i>	(Cockerell, 1929)	<i>T. habropodae</i>	(Cockerell, 1929)	Co-flight	Cockerell 1929
<i>H. christineae</i>	Dubitzky, 2007	<i>T. heinzi</i>	Dubitzky, 2007	Elev., phenology, dist.	Dubitzky 2007
<i>H. buconis</i>	(Friese, 1911)	<i>T. himalayana</i>	(Bingham, 1897)	Distribution	Dubitzky 2007
<i>E. erratica</i>	(Lieftinck, 1944)	<i>T. insidiosa</i>	(Lieftinck, 1944)	Co-flight	Lieftinck 1944
<i>E. impatiens</i>	(Lieftinck, 1944)	<i>T. vulpecula</i>	(Lieftinck, 1944)	Co-flight	Lieftinck 1944
<i>H. xizangensis</i>	Wu, 1979	<i>T. himalayana</i>	(Bingham, 1897)	Co-flight, abund., dist.	This study
<i>H. mimetica</i>	Cockerell, 1929	<i>T. mimetica</i>	Orr & Zhu, sp. nov.	Co-flight, abund., dist.	This study

marily on range overlap and concurrent collections, a total of five specific host-parasite associations have been suggested for *Tetralonioidella* (Table 1). Unfortunately, direct evidence of host associations remains elusive for this group due to their rarity.

Although *Tetralonioidella* was originally described as a genus over a century ago (Strand 1914), it was not until Lieftinck (1983) rediscovered the name and moved ten species into this taxon that it was widely used. More recently, Dubitzky (2007) and Niu et al. (2017) treated the species of Taiwan and mainland China, respectively. Unfortunately, despite recent efforts, the taxonomy of this rare genus remains problematic, as is exemplified by the fact that 9/19 species of *Tetralonioidella* lack female descriptions while another 2/19 lack descriptions for males in recent work (Niu et al. 2017; note there are 20 total with this paper). These various issues are further compounded by the large number of additional species expected to be recorded in China (Orr et al. 2022). For difficult groups such as these, integrative taxonomic methods incorporating multiple lines of evidence such as morphological and molecular data becomes especially valuable (Orr et al. 2020).

As part of an initial, systematic treatment of the group we here describe a new mimetic species, *Tetralonioidella mimetica* Orr & Zhu, sp. nov., and confirm its generic placement based on morphological and molecular analyses, the latter of which is also used to preliminarily investigate the relationships of the genera within Melectini. The remaining *Tetralonioidella* are then reviewed for additional mimics and potential hosts and mimicry models are discussed for these species. Where relevant, these are assigned to bumble bee color patterns to enable comparison with their geographic ranges. Finally, we briefly consider the phenomenon of mimicry among other Asian bees, with special focus on the Chinese fauna.

Materials and methods

Systematics

A total of seven specimens (three females, four males) of the new species were examined. All specimens directly examined are deposited in the Institute of Zoology, Chinese Academy of Sciences, Beijing (IZCAS), including the holotype and paratype of the new species. Where possible, type specimens were directly examined for other

species (9/19 species, the Chinese species), and otherwise reference was made to imaged type specimens (2/19: *Tetralonoidella habropodae* (Cockerell, 1929) and *Tetralonoidella pendleburyi* (Cockerell, 1926)), specimens (2/19), other images (4/19), and original descriptions (2/19) to ensure that the species focused on here is new and to discern whether other species represent mimics.

The terminology used largely follows that of Michener (2007) and Niu et al. (2017). Abbreviations used include: F = flagellomere, T = tergum, S = sternum. Images were taken using various equipment as follows: description and general morphological characters of the new species with an Olympus OMD EM1 firmware 4.4 using an Olympus Zuiko 60mm f:2.8 macro, other images including genitalia with a Canon EOS80D. Some images were brightened in post-processing to better approximate real-life color depth.

Sampling of sequence data

We constructed a backbone phylogenetic hypothesis using character-rich Ultra-Conserved Element (UCE) data, which was subsequently expanded with placement of additional species represented by COI barcodes only. For UCEs, nine species of Melictini were acquired from Sless et al. (2022) and re-analyzed with *Tetralonoidella* as the sister-group of the remaining melictine taxa, given its accepted phylogenetic placement (Sless et al. 2022). For COI, a total of 12 sequences representing minimally 10 species across five genera was taken from GenBank (NCBI) and the Barcode of Life Database (BOLD), including an outgroup from Anthophorinae (Table 2). Eight additional COI sequences were taken from a recent UCE study on the apid subfamily Nomadinae (Sless et al. 2022). An additional four new COI sequences of rare species were generated for this study using standard barcoding approaches (as in Orr et al. 2018). Accession numbers for all sequences are given in Table 2.

Phylogenetic analyses

We used the aligned UCE matrix of Sless et al. (2022) and parameters are given therein. Maximum likelihood reconstructions of the UCE data were performed using IQ-TREE v1.6.12 (Nguyen et al. 2015) with 1,000 ultrafast bootstraps (UFBoot, Hoang et al. 2018), 1,000 SH-aLRT replicates (Guindon et al. 2010), and best substitution model “GTR+F+R2” within IQ-TREE. A secondary phylogenetic analysis was conducted with the COI data, using the UCE result as a backbone. Effectively, the UCE data were used to constrain the relationships recoverable in a barcode tree, with special focus on older nodes where barcode data generally provide unreliable results. Nine species were represented in both the barcode and UCE data. Barcodes were aligned using Clustal Omega version 1.2.4 (Madeira et al. 2022), with the alignment of 26 sequences totaling 737 columns (365 distinct patterns, 290 parsimony-informative, 60 singleton sites, and 387 invariant sites). These were constrained in the COI inference (Zhou et al. 2016) by inputting the Newick format result of the UCE analysis as a partial constraint tree with the *-g* switch of IQ-TREE.

Table 2. Specimens sequenced. Columns given include published ID number, tribe, genus, species, and the source via which it can be queried. In the source, “here” refers to this paper and in such cases provides the pre-upload voucher code of the sample. GB refers to uploads on GenBank, and BOLD refers to uploads on the Barcode of Life Database.

ID	Tribe	Species	Source
CCDB-15281	Anthophorini	<i>Pachymelus peringueyi</i>	BOLD
BEECC863-09	Melectini	<i>Melecta alexanderi</i>	BOLD
BBHYG927-10	Melectini	<i>Melecta pacifica</i>	BOLD
BEECC859-09	Melectini	<i>Melecta separata</i>	BOLD
BEECC754-09	Melectini	<i>Melecta thoracica</i>	BOLD
BEECB476-07	Melectini	<i>Brachymelecta californica</i>	BOLD
BEECC854-09	Melectini	<i>Zacosmia maculata</i>	BOLD
KJ839671	Melectini	<i>Melecta albifrons</i>	NCBI
KJ839507	Melectini	<i>Melecta luctuosa</i>	NCBI
HM401245	Melectini	<i>Thyreus orbatus</i>	NCBI
EX037	Melectini	<i>Melecta albifrons</i>	Sless et al. 2022
EX036	Melectini	<i>Melecta italica</i> cf.	Sless et al. 2022
BLX881	Melectini	<i>Melecta thoracica</i>	Sless et al. 2022
EX042	Melectini	<i>Tetralonoidella pendleburyi</i>	Sless et al. 2022
EX044	Melectini	<i>Thyreomelecta sibirica</i>	Sless et al. 2022
EX088	Melectini	<i>Thyreus delumbatus</i>	Sless et al. 2022
EX090	Melectini	<i>Thyreus quinquefasciatus</i>	Sless et al. 2022
EX029	Melectini	<i>Brachymelecta californica</i>	Sless et al. 2022
D0863	Melectini	<i>Eupavlovskia obscura</i>	Here: MGPCC007-21 (BOLD)
D08632	Melectini	<i>Eupavlovskia obscura</i>	Here: MGPCC008-21 (BOLD)
IOZ(E)2148081	Melectini	<i>Tetralonoidella mimetica</i>	Here: MGPCC191-24 (BOLD)
IOZ(E)2148051	Melectini	<i>Tetralonoidella wuae</i>	Here: MGPCC192-24 (BOLD)
BSRUAA6806	Melectini	<i>Thyreus callurus</i>	Here: PQ074116 (GB)
BSRUAA6807	Melectini	<i>Thyreus centrimaculata</i>	Here: PQ074117 (GB)
BSRUAA6787	Melectini	<i>Thyreus ceylonicus</i>	Here: PQ074119 (GB)
BSRUAA6780	Melectini	<i>Thyreus himalayensis</i>	Here: PQ074118 (GB)
BSRUAA6801	Melectini	<i>Thyreus cyathiger</i> cf.	Here: PQ074120 (GB)

We compared the likelihood of this result with other hypotheses to evaluate the generic associations and validity of the taxa included here (with our tree considered *hypothesis 1*, to see whether alternative scenarios were significantly better supported than our reconstruction when they were imposed via constraints). First, we tested whether *Melecta* was monophyletic without the tentative subgenus *Melecta* (*Eupavlovskia*) Popov, 1955 (*hypothesis 2: Melecta* monophyletic). We then tested whether (*Eupavlovskia*) also belonged within the genus *Melecta* as considered by Michener (2000, 2007) (*hypothesis 3: Melecta* monophyletic, with (*Eupavloskia*) as a subgenus). The latter two hypothesis scenarios were implemented with manually defined constraint files input to IQ-TREE as previous. Each of the three inferences incorporated model testing (Kalyaanamoorthy et al. 2017), with model TIM+F+I+G4 selected based on both the Akaike Information Criterion and Bayesian Information Criterion. The likelihood of the three hypotheses was compared with the approximately unbiased (AU) test, with 10,000 multiscale bootstrap replicates (Shimodaira 2002).

Results

Phylogeny

The backbone phylogeny provided generally reliable results for the groups of interest in Melectini (Fig. 1). As according to Sless et al. (2022), the genus *Tetralonoidella* was sister to the genus *Eupavlovskia* and both lineages together form the sister group to the remaining Melectini. The small genus *Zacosmia* Ashmead, 1898 was then sister to a well-supported group with the remaining melectine genera, where *Thyreomelecta* Rightmyer & Engel, 2003 was sister to *Thyreus*, with those two genera sister to *Melecta* + *Brachymelecta* Linsley, 1939. This latter group appears problematic, with a poorly supported grouping of several Eastern and Western Hemisphere species of *Melecta* recovered as sister to a clade comprising *Brachymelecta* and another clade of *Melecta* from both the Eastern and Western hemispheres. These results were generally consistent with Sless et al. (2022), save for the issues in *Melecta*, which is expected given that a subset of those data was used for the backbone.

Topological tests provided definitive insight into the placement of *Eupavlovskia*, strongly supporting it as separate from *Melecta* (Suppl. material 1: table S1, note S1), where it had previously been considered as only a subgenus by Michener (2000; 2007). However, as well as being originally described as a distinct genus, *Eupavlovskia* was also considered to be a valid genus by Lieftinck (1969; 1972; 1983), the last major reviser of Old World Melectini. Consequently, we return to the position of Lieftinck and restore *Eupavlovskia* to the generic level now with a phylogenetic justification, providing an account below in the Systematics subsection. Contrastingly, the results for whether or not *Melecta* was paraphyletic in relation to *Brachymelecta* were inconclusive (Suppl. material 1: table S1, note S1). As such, we choose not to take formal action on the status of *Melecta*; instead, we prefer to improve taxon sampling in future efforts to address the lingering possibility of *Melecta* not representing a monophyletic group.

Generic placement of the new species

The placement of the new species was initially difficult because it exhibited characteristics of both *Tetralonoidella* and *Eupavlovskia*. The exceptionally long forewing marginal cell supports the placement of this species in *Tetralonoidella*, following Michener's (2007) interpretation. However, a specimen of this species collected in 1993 from the IZCAS collection was labeled as "*Eupavlovskia* sp.". Both sexes were present, and this error was likely based on the distally enlarged and flattened hind basitarsus of the male (Fig. 2). As this character can also be found in *Melecta* (*Melecta*) and *Melecta* (*Paracrocisa*) Alfken, 1937, it does not appear to be uncommon or phylogenetically conserved in Melectini. Further, this species clearly agrees with the generic diagnoses of *Tetralonoidella* in Dubitzky (2007), Michener (2007), and Niu et al. (2017). Finally, the phylogenetic evidence presented herein clearly places the new species within *Tetralonoidella* with strong support, as detailed above, giving us confidence in this placement and highlights the need to better delineate *Eupavlovskia*.

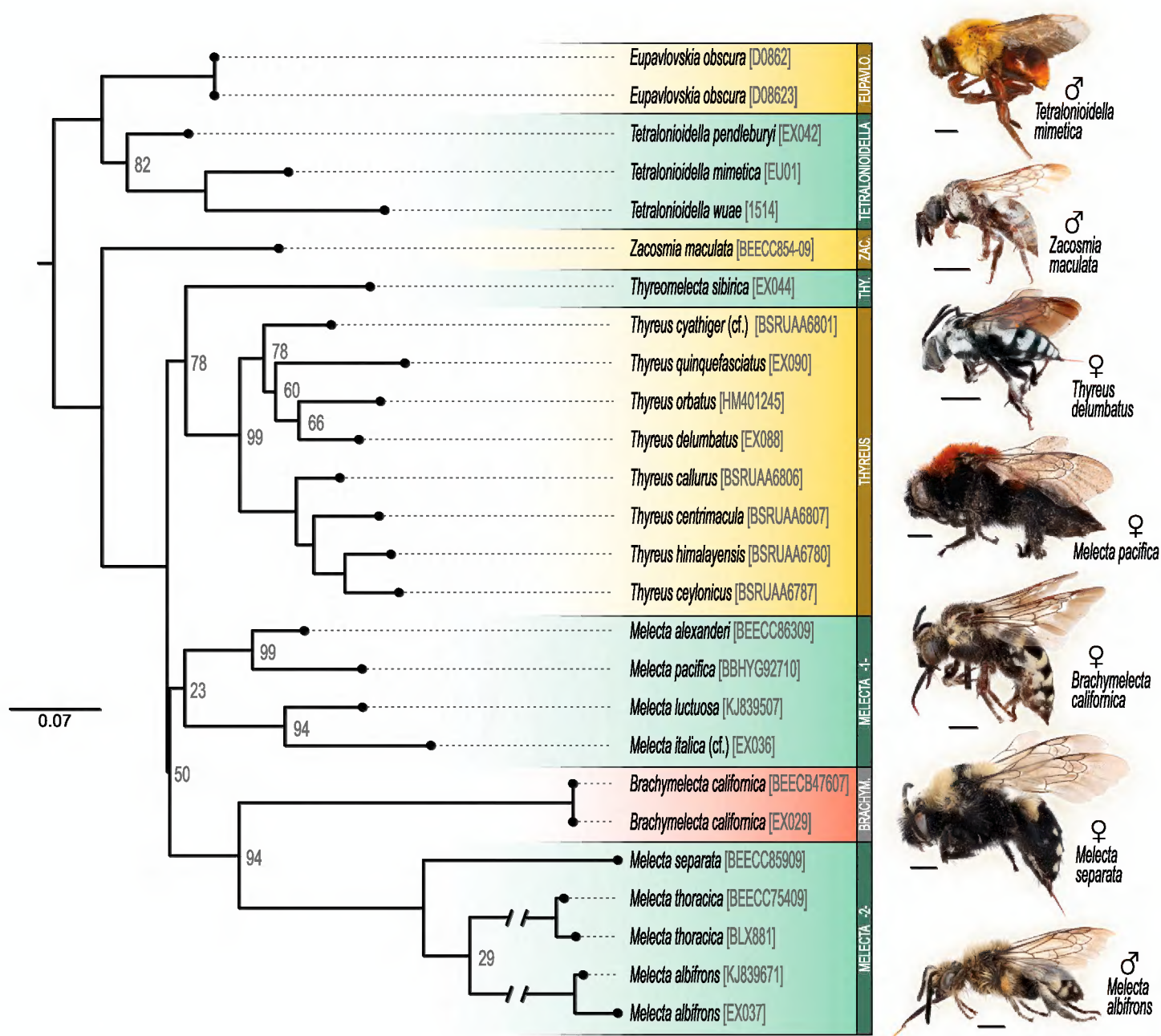


Figure 1. Phylogeny of Melectini. The tree was inferred using UCE and COI sequence data. Values at nodes are bootstrap support values and left scale bar refers to substitutions per site. Scale bars next to specimens indicate 2 mm length. Sequence identifiers are giving following species names.

Systematics

Superfamily Apoidea

Family Apidae

Subfamily Nomadinae

Tribe Melectini

Eupavlovskia Popov, 1955, stat. rev.

Melecta, sensu Michener 2000, 2007 (former subgenus).

Diagnosis. Diagnosis is best made in the male sex, as there are no known characters present in the female sex which allow unambiguous separation from all other melectine genera. Generally robust, moderately large bees, 12.5–16 mm in length. Mesosoma

covered with long and dense pubescence, this particularly evident on the dorsal surface where it covers and obscures the pronotal tubercles, scutum, scutellum, and scutellar spines. Marginal cell of forewing short, three times as long as broad, only slightly exceeding the third submarginal cell. Labrum almost square, widest basally, surface slightly concave, anterior border entire, little upturned, with rounded side edges, basal tubercles only weakly projecting but generally large. Hind tibia of the male strongly broadened and expanded at its apex, with strong ventroapical process extending laterally beyond the base of the tibial spurs. Inner hind tibial spur noticeably longer than the outer, gently and variably curved in different directions, appearing weakly undulate. Hind basitarsis of the male strongly to moderately broadened in its apical half to two-thirds. Male antennae without rhinarial pits on their posterior faces (*sensu* Lieftinck). T7 of male subtruncate, apex clothed with appressed tomentum. S7 very slender, with narrow, widely divergent arms and bilobed apex, the lobes fringed with strong bristles; S8 with well-developed ridges in apical half, apex itself with tufts of long feathery hairs.

Due to the thickly hairy mesosoma, *Eupavlovskia* can appear superficially quite similar to *Tetralonioidella*, but they may be separated by a short marginal cell (the most common character state for melectine bees) that only extends slightly beyond the apex of the third submarginal cell, the marginal cell itself being clearly shorter in maximum length than the length of the three submarginal cells combined; it is also shorter than the distance between its apex and the apex of the forewing. In *Tetralonioidella* the marginal cell is much longer, exceeding the third marginal cell and only slightly shorter than the length of the three submarginal cells combined; it is longer than the distance between its apex and the apex of the forewing. From other Eastern Hemisphere melectine bees, *Eupavlovskia* is separated by the scutellum, which is not flattened into a plate that overhangs the declivity of the propodeum and by the presence of arolia (with a plate-like scutellum and without arolia in *Thyreus*), by the three submarginal cells (two submarginal cells in *Sinomelecta* Baker, 1997), by the length of T1, which is dorsally shorter than T2 and the presence of arolia (T1 longer than to scarcely shorter than T2 dorsally and with arolia absent or nearly so in *Afromelecta* Lieftinck, 1972 and *Thyreomelecta*), from all *Melecta* or currently recognized *Melecta* subgenera by the combination of the long and dense mesosomal pilosity, the shape of the male legs, the absence of rhinaria on the antennal segments, and the structure of the male S7–8.

Distribution. From Spain in the west across the Western Palearctic to Central Asia (Uzbekistan, Bukhara; Lieftinck 1969). Not present in Africa or the Levant. Composed of two species, *Eupavlovskia funeraria* (Smith, 1854) from Spain to the Caucasus and *Eupavlovskia obscura* (Friese, 1895) from Italy to Uzbekistan.

Comments. *Eupavlovskia*, *Paracrocisa* and *Pseudomelecta* Radoszkowski, 1865 were separated from *Melecta* at the generic level by Lieftinck (1969; 1972; 1983), but Michener (2007) considered the given characters insufficiently distinctive and instead considered them as subgenera. We show here that *Eupavlovskia* is valid and separate from *Melecta* and its other groups (via molecular work here and prior morphological accounts), and formally return it to the generic level once more; further work is necessary on the rare groups *Melecta* (*Paracrocisa*) and *Melecta* (*Pseudomelecta*) to ascertain whether they also warrant generic-level treatment.

***Tetralonoidella mimetica* M. C. Orr & C. D. Zhu, sp. nov.**

<https://zoobank.org/DE741BE9-30F8-4C28-A16C-CB22D673E2F3>

Tetralonoidella mimetica Orr & Zhu, 2023: holotype (IOZ(E)2148141): male: male, holotype: China, Sichuan Province, Wenchuan City, Yingxiu County, 900 m, 1983.8.3, coll. Zhang Huaicheng. Verbatim: 四川汶川映秀 900m // 1983, 8.3张怀成 // IOZ(E)2148141. Translation: Sichuan Province, Wenchuan City, Yingxiu, 900m // 1983.8.3 Zhang Huaicheng // IOZ(E)2148141. Coordinates from Google Earth retroactive georeferencing: 31.05, 103.49.

Diagnosis. The forewing marginal cell is clearly longer than the distance from its apex to the apex of the forewing, and this character separates it from other melectine genera. Additionally, both sexes are immediately recognizable from nearly all other Melectini by color, specifically the yellow scutellar hair followed by a largely black metasoma tipped with reddened terga and hairs. Among melectines, it may still be confused with *Tetralonoidella tricolor*, from which both sexes can be distinguished by a transverse black stripe of hair on the scutum, and in males additionally by the unmodified hindleg of *T. tricolor* compared to the enlarged, flattened hindbasitarsus of the new species.

In the key of Niu et al. (2017), females run to couplet 7 but clearly do not fit the color patterns described. Males key to couplet 19 and their S8 more closely resembles that of *T. tianmuensis*, though with a much stronger medial point. Some males with brighter scutal setae color may key instead to *Tetralonoidella fukienensis* Lieftinck, 1983. In both cases, pubescence color of *T. mimetica* clearly distinguishes it from the alternatives.

Description. Male: pubescence and integumental color: See Figs 2, 3. Closely resembling bumble bee coloration, specifically group 134 of Williams (2007). Head black, integument of galea medium brown, mandibles dark brown, labrum medium brown-reddish, and sometimes clypeal edges dark brown. Mesosoma yellow over largely black integument. Legs brown to light brown, slightly lighter than primarily dark brown integument. Metasomal T1-2 black, sometimes reddened slightly on edge of T2. T3 onward increasingly reddish-orange in integument and pubescence, wholly so typically by T4. Metasomal sterna following terga, though starting at dark brown.

Males smaller, body size 12–13mm.

Head: Galea only slightly longer than height of eye, shiny throughout, with minute single-sized punctures, tip angularly pointed but sides rounded to tip. Mandible unmodified, with weak but distinct inferior blade running parallel to main blade. Labrum shiny but somewhat craggy, large punctures indistinct from various angles, rim shallowly but obviously, roundly indented medially, with distinct row of hairs along rim though not forming dense brush. Lacking facial maculations. Clypeus strongly protuberant, by about half max eye width. Clypeus shiny medially near rim, tessellate elsewhere, with distinct rounding outward above shiny rim, with irregular but dense pitting throughout. Cheek immediately slanted inward from rear of compound eye. Antennal F1-2 roughly equal length, slightly longer than subsequent flagellomeres. Ocelli nearly linear, medial ocellus only slightly lower than lateral ocelli. Integumental

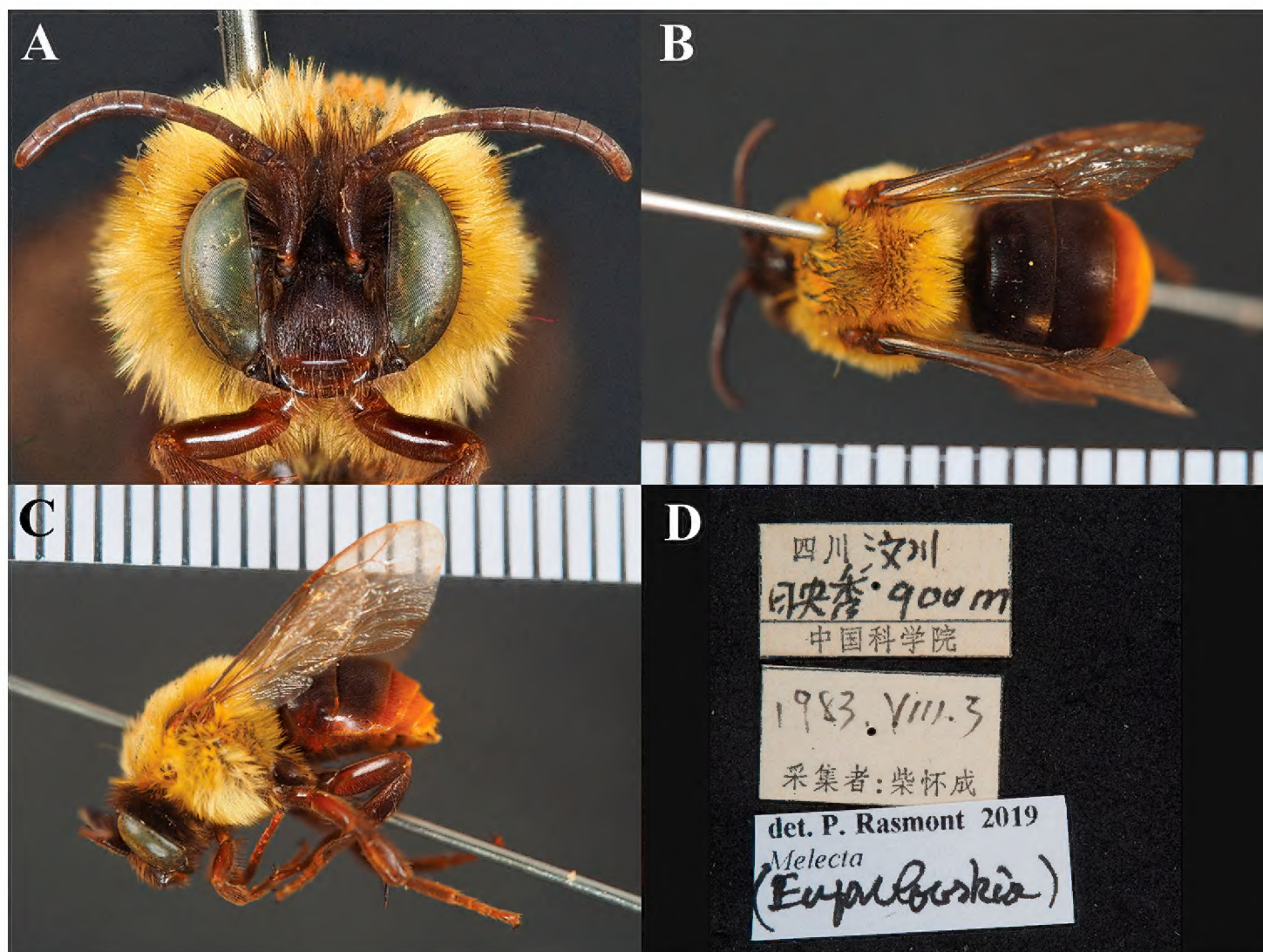


Figure 2. Male external morphology of *Tetralonioidella mimetica* sp. nov. Imaged from the holotype (IOZ(E)2148141) **A** face **B** dorsal **C** habitus **D** labels excluding identification label. Lines represent mm. Images by PR.

surface near ocelli shiny, strongly pitted below, slightly tessellate and sparsely, minutely pitted between lateral ocelli and compound eye.

Mesosoma: Intertegular distance (at rear) averaging 3.58 mm based on four specimens (3.5, 3.6, 3.5, 3.7). Wings only very slightly darkened, hairy within cells along fore edge and decreasingly so posteriorly, apical papillae strongly apparent. Scutum, scutellum, metanotum typically obscured by dense, plumose hair. Below, integument densely punctured, interspaces weakly tessellate. Tegula translucent, medium brown, somewhat orange. Scutellar spines large, strongly pointed and directed posteriorly and slightly laterally, still obvious through dense hairs although eclipsed by them. Legs largely unmodified, save for hindleg: tibia in profile increasing in width from unmodified base to tip that is over twice its initial width, vaguely triangular overall, not flattened, broadest apically. Hindbasitarsus similarly narrow proximally, though flattened and broadened to tip like a paddle. Basitibial plate absent.

Metasoma: T1-2 longer from above, about equal, with T3 at most roughly 2/3 of either. Terga covered in small hairs, largely simple medially but increasingly plumose laterally and apically, largely plumose by T4. Terga weakly tessellate between punctures, with weak reflections; usually apparent through appressed setae for T1-2 and often T3. Tergal rims unmodified, of similar opacity, color to rest. Male T6 unmodified.

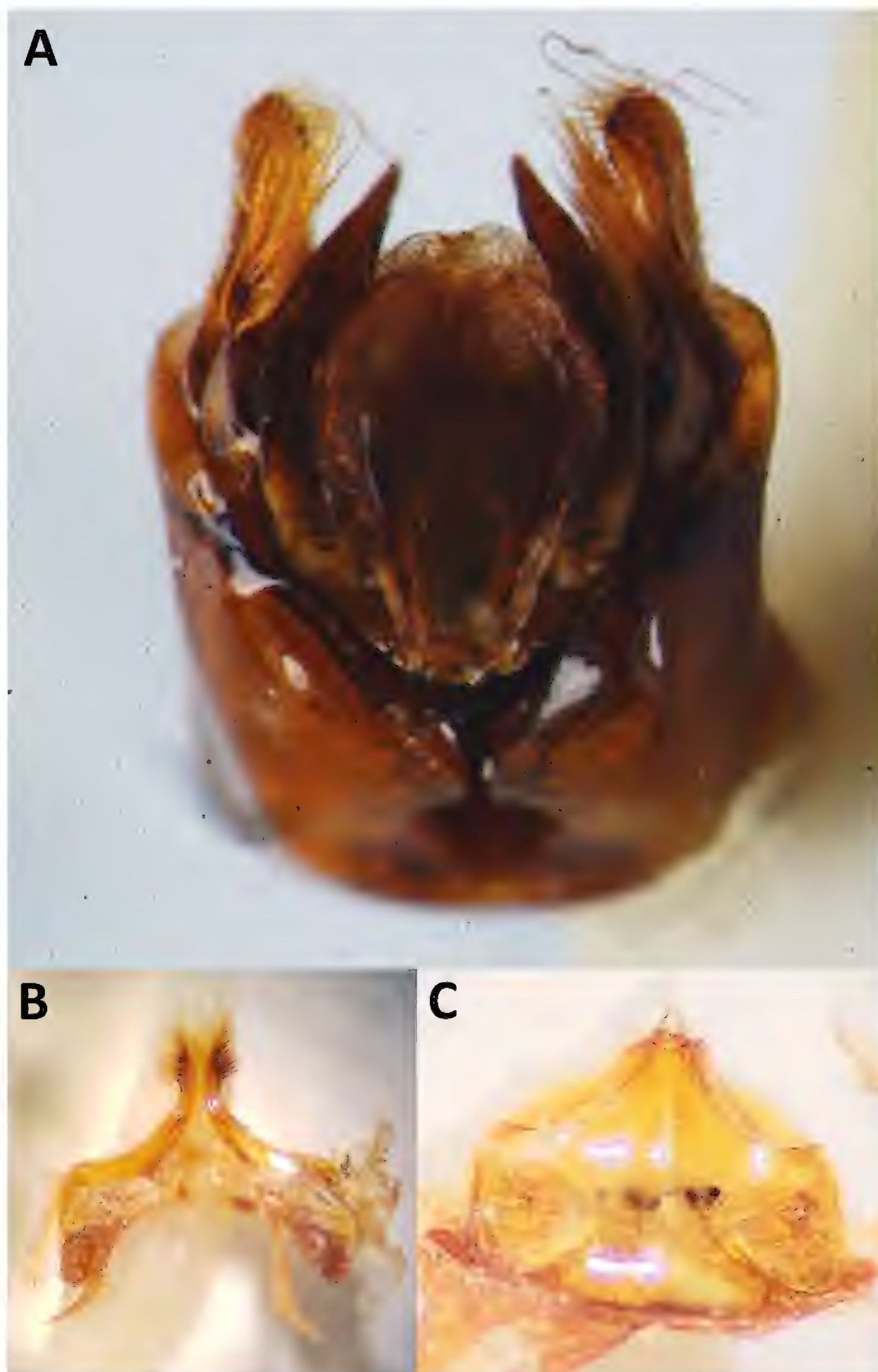


Figure 3. Male genitalia of *Tetralonioidella mimetica* sp. nov. Imaged from IOZ(E)2148161 **A** genital capsule (brightened, ~80×) **B** S7 (50×) **C** S8 (50×).

Male T7 in profile gradually thinning to tip with slight abrupt dip medially; without medial longitudinal carina, but covered in dense hairs beyond base; lacking lateral projections or flanges; tip from above bilobed with medial indentation similar in size to each of the lobes, with rounded tip. Male S6 unmodified and lacking distinctive hair patches, very slightly and gradually shallowed medially along rim. Male S7 overall initially appearing disconnected medially given weak medial scleritization contrasting with stronger tan integumental color laterally; with distinct lateral corners nearing 90°, but rounded; with strong subapical hair tufts directed laterally; tip broadly bifid with wide pointed tips, lateral to broad apical, V-shaped emargination. Male S8 shield-like, laterally gradually declivous in latter half though maintaining overall rounded outline until near tip, there projected forward and narrowing to tip, sharply pointed medially with long hairs arising from below. Male genital capsule with outer corners, where gonocoxite tips curve inward to gonostylus, lacking any flange, instead marked by narrowing toward tip, though again slightly expanded terminally, largely without hairs. Interior projection between gonostylus and penis valves also narrowed to tip, but entirely covered in long, plumose hairs largely obscuring form.

Female: highly similar to males overall, differing as given: Pubescence and integumental color: See Fig. 4. Head generally slightly darker through, save glossa and labrum. Leg hairs darker, more often black or dark brown, integument similar.

Females slightly larger, in part due to more tapering, elongate metasoma, body size 13–14mm, largest nearing 16mm.

Head: labrum more narrowly and abruptly indented medially, forming clearer corners.

Mesosoma: Intertegular distance (at rear) similar, averaging 3.63mm based on three specimens (3.8, 3.5, 3.6). Legs unmodified, hind tibia only slightly expanded apically, with widest point clearly before tip.

Metasoma: Overall shape roughly similar but tapering to more distinct point terminally. T1-5 visible from above, T6 typically only visible for pygidial plate, itself triangular near base, coming to narrow tip with near-parallel sides. Sterna largely unmodified, last visible sterna narrowed and curled upward, elongate, forming support for very long sting.

Distribution. This species is recorded from Sichuan (four sites), Guangzhou (one site), and Hunan (one site) at elevations of 700 m, 700–900 m, 900 m, 1150–1200 m, 1270 m, and 1300 m (relatively low for Sichuan bumble bees, Williams et al. 2009). Notably, this species has not been found on the Qinghai-Tibetan Plateau or the lower elevations of the Sichuan depression (the latter absence could in part be due to local landscape alteration). This bee might be restricted to mid-elevations as such, below the edge of the nearby Qinghai-Tibetan Plateau, although we cannot yet determine any type of habitat specificity with the little data available.

Phenology. This bee has been collected from July 24 through August 18.

Bee hosts. *Habropoda mimetica* Cockerell, 1927 is the most likely host, based on similarities in known distribution (mid-elevation ringing Sichuan depression and adjacent similar habitat), phenological matching, and elevational similarity. This association was especially evident at the Baishuihe National Nature Reserve in Sichuan, where



Figure 4. Female external morphology of *Tetralonioidella mimetica* sp. nov. Imaged from IOZ(E)2148071 **A** face **B** dorsal **C** habitus **D** labels excluding ID label. Lines represent mm. Images by PR.

H. mimetica was exceedingly common, while other species of *Habropoda* were rarer (*Habropoda omeiensis* Wu, 1979, *Habropoda sinensis* Alfken, 1937). It may be that this species targets multiple hosts, but among these *H. mimetica* is almost certainly utilized.

Floral visitation. No floral data are available for this species. Brood parasites are generally considered relatively generalist, given that they need not collect pollen for their offspring, but tracking specific resources may benefit a brood parasite in finding specialized hosts.

Etymology. The name “*mimetica*” is given to reference its mimicry and also its likely host, *Habropoda mimetica*. This name derives from the Ancient Greek adjective *mimetikos* (that which imitates), and is in the feminine singular nominative form.

Material examined. All are paratypes except for the holotype: IOZ(E)2148141: male, holotype: China, Sichuan Province, Wenchuan City, Yingxiu City, 900 m, 1983.8.3, coll. Zhang Huaicheng; IOZ(E)2142171: male: China, Chongqing City, Wanzhou District, Wangerbao National Nature Reserve, 1300 m, 1993.8.15, Song Shimei; IOZ(E)2148161: male, genitalia pulled: China, Guizhou Province, Tongren City, Shiqian County, Jinxing village, 700 m, 1988.7.24, coll. Yang Longlong; IOZ(E)2148151: male: China, Hunan Province, Xiangxi Tujia and Miao Autonomous Prefecture, Yongshun County, Muhe Forest farm, 700–900 m, 1988.8.8, coll.

Yang Longlong; IOZ(E)2148081: female, EU1 COI voucher: China, Sichuan Province, Baishuihe National Nature Reserve, 31°15'56"N, 103°50'02"E. 2018.8.17, coll. Feng Yuan; IOZ(E)2148071: female: Sichuan province, Chengdu City, Pengzhou City, Xiaoyudong Town, Longcaogou (Baishuihe National Nature Reserve), 31°13'39"N, 103°45'05"E, 1150–1200 m, 2018-VIII-18; IOZ(E)2148061: female: Sichuan Province, Wenchuan City, Yingxiu County, 900 m, 1983.8.3, coll. Zhang Huaicheng.

Comments. The new species was originally set aside by Yan-Ru Wu as a member of *Eupavlovskia*, later identified as a possible *Tetralonioidella* by MCO and ZN and then hypothesized to be *Eupavlovskia* again by PR.

Review of mimicry patterns of species of *Tetralonioidella*

Bumble bees seem the most likely model in this system. Given the complexity of the color patterns detailed herein, it seems unlikely that they have arisen and been maintained by chance, or by aposematism as might be the case for some all-black, red-tailed species (Williams 2007). Bumble bees are commonly mimetic models for a wide range of taxa (Willadsen 2022; Chatelain et al. 2023), including for each other (Williams 2007; Williams 2008). This is likely a consequence of their sociality and defensiveness at nests, their generally high willingness to sting compared to solitary bees, the distinctiveness of their often-vibrant color patterns, and their high abundance in some environments. As another social and abundant group of bees, honey bees are similarly mimicked by a wide variety of taxa (Rettenmeyer 1970; Chatelain et al. 2023), and the same happens with various social wasps (Chatelain et al. 2023). From these facts, when mimetic systems exist incorporating bumble bee color patterns, it seems reasonable to assume that bumble bees serve as models (so long as other aggressive, social, abundant species are not involved).

If we accept that *H. mimetica* is the host or one of the hosts of *T. mimetica*, and that *Bombus* are the likely models in this system, then this species represents a three-tiered mimicry complex, comprised of the model bumble bee(s), the host *H. mimetica*, and the brood parasite *T. mimetica*. In this case, there are many potential bumble bee models, but the most likely models are species including *Bombus breviceps* Smith, 1852 and *Bombus trifasciatus* Smith, 1852, based on coloration, distribution, and commonness (Williams et al. 2009). To our knowledge, this is the first documented case of three-tiered mimicry in bees, comprised of model host-brood parasite. An additional potential member of this mimicry ring at the brood parasite level is the species *Tetralonioidella tricolor* (Lieftinck, 1972), which may be separated from *T. mimetica* by the transverse black hair band across the scutum and the unmodified male hind leg, but the host of that species remains unknown although both *Tetralonioidella* species are found in the same general region.

Further investigation of other *Tetralonioidella* species revealed two additional potential examples of three-tiered mimicry (Fig. 5). The first of these is detailed by Cockerell (1929), where he documented *Tetralonioidella habropodae* flying with *Habropoda sutepensis* Cockerell, 1929 at Doi Sutep mountain in Thailand, from which he infers not only resemblance but also a host association between the two. Although he does not note it, these two species also strongly resemble lighter individuals of *Apis cerana* Fabricius, 1793 which is found in

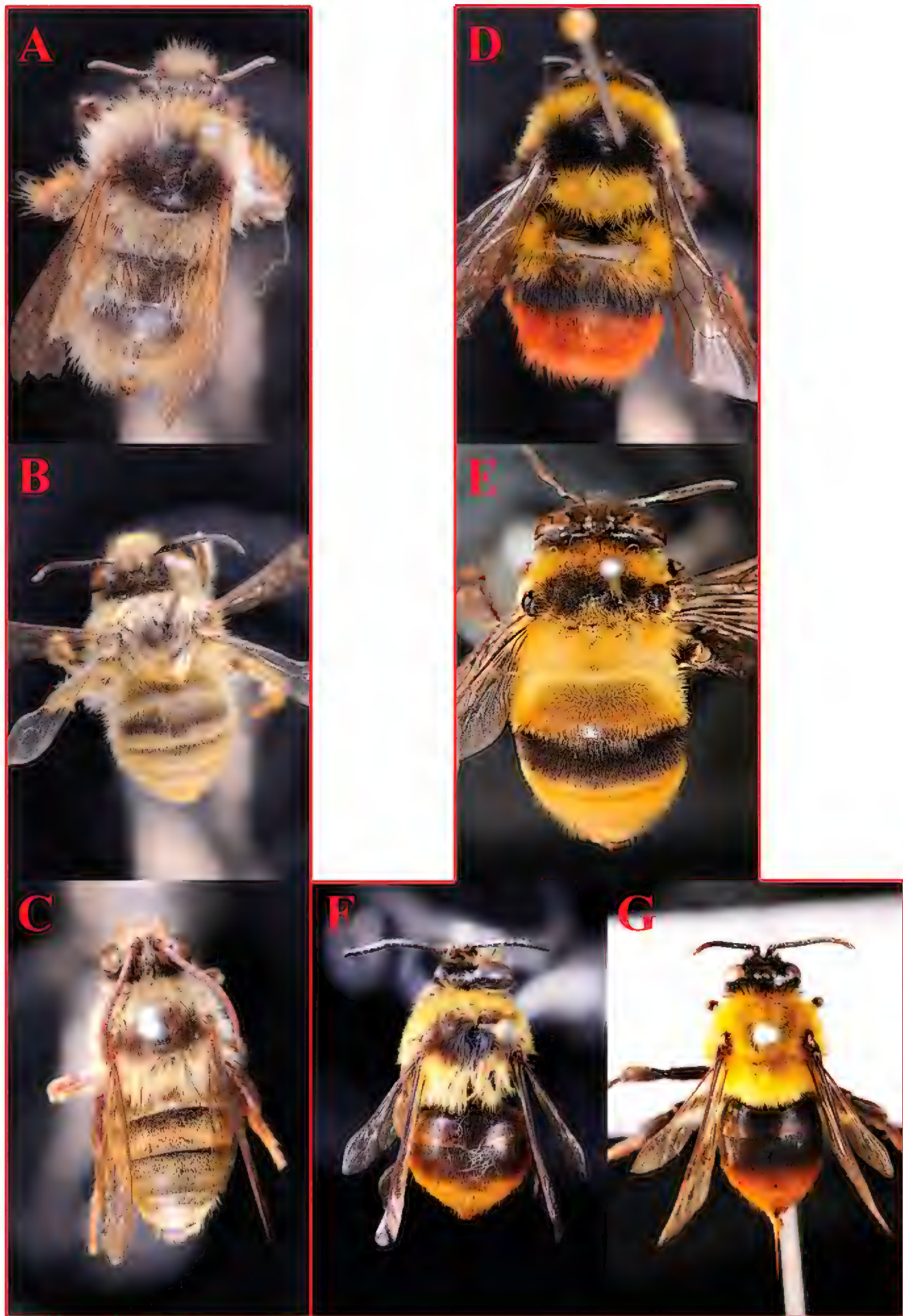


Figure 5. Hypothesized examples of three-tiered mimicry systems in bees. Given are the model (top), likely host (middle), and brood parasite (bottom). System 1: likely model **A** *Bombus lepidus* worker (IOZ(E)1429818); likely host **B** *Habropoda xizangensis* male (IOZ(E)2051720); and brood parasite **C** *Tetralonioidella himalayana* male (IOZ(E)2148111). System 2: likely model **D** *Bombus friseanus* worker (IOZ(E)1429817); likely host **E** *Habropoda mimetica* female (IOZ(E)2148091); and brood parasites **F** *Tetralonioidella tricolor* male (IOZ(E)2148051) **G** *Tetralonioidella mimetica* female (IOZ(E)2148071). Note that multiple species may act as models or hosts.

the region, making this a potential three-tiered mimicry system. The third example is newly proposed here and more tenuous, focused on the unusually widespread *Tetralonioidella himalayana* (Bingham, 1897) (found in the Himalaya, and inexplicably also Taiwan, with few records in-between). Because of its large range, this parasite must be attacking multiple *Habropoda* species. Among these, the Himalayan *Habropoda xizangensis* Wu, 1979 presents one of few host options covering the western range of *T. himalayana*, and notably that species exhibits an unusual olive-colored hair patterning similar both to and bumble bees of the *Bombus lepidus* Skorikov, 1912 group.

The species of *Tetralonioidella* with yellow scutal hair and largely black metasomas (e.g., *T. pendleburyi*, etc.) may also represent mimics of other bees such as *Xylocopa appendiculata* Smith, 1852, which can be quite common (although more so in or near human habitats). However, this will require further study, as it is an exceedingly common color pattern across various groups of bees, and it is unclear whether this is a result of mimicry (although suggested as such in Wilson et al. 2022).

Discussion

Systematics

The present study highlights the need to solidify and expand our understanding of melectine systematics and taxonomy. As an important first step, we provide a framework and method for integrating data types, which, going forward, will enable quicker and more efficient phylogenomic works on this and other understudied groups for which phylogenomic data are lacking but where many barcodes are available. This is especially important in developing countries where many new species are expected to be present, but where the capacity for phylogenomic sequencing and analysis remains limited (Orr et al. 2020). The biggest remaining challenge is to understand the true limits of the genus *Melecta*, as the name is ascribed to the genus type-species *Melecta albifrons* (Forster, 1771) (West Palearctic), which we found to group most closely related to several Western Hemisphere species (Fig. 1, *Melecta* clade ‘1’). This clade forms the sister group to the Western Hemisphere genus *Brachymelecta*, which renders *Melecta* paraphyletic: an additional clade of primarily Eastern Hemisphere species (Fig. 1, *Melecta* clade ‘2’) form the sister group to *Melecta* clade 1 + *Brachymelecta*. Given the comparatively low supports in this region of the tree, however, we must sample additional taxa and ideally generate more UCEs or low-coverage genome data to better solidify these relationships and understand what other names, if in fact necessary, must be raised to the generic level. *Thyreus* should also be further investigated, as there are many species (>200), and it remains uncertain if the much smaller genus *Thyreomelecta* is valid and distinct.

There are some additional, more recent taxonomic actions which also require further treatment. This year, Dohling and Day (2024) described *Tetralonioidella meghalayensis* Dohling & Day, 2024 from four female specimens from north-eastern India (Meghalaya state), but the holotype specimen that they imaged is a pollen-collecting bee

based upon its visible scopa on the hind legs (see their figs 1, 3). It cannot be *Tetralonioidella*, as all these brood parasitic species lack scopae. From the character examination (including wing venation, with the 1st and 2nd recurrent veins meeting the 2nd and 3rd submarginal cross veins, respectively) and myriad other features, it clearly belongs to the anthophorine genus *Habropoda*. Further comparison with Lieftinck (1974) and pinned reference material at Naturalis by TJW confirms that not only is it *Habropoda*, but that it fits clearly within the distribution of, and morphological variation seen in *Habropoda radoszkowskii* (Dalla Torre, 1896) (clypeus medioapically with a small but distinct and narrowly triangular yellow mark (not transverse), face with dense adpressed to erect whitish hairs on paraocular areas and frons, terga without clearly defined pale apical hairbands, body pubescence reddish, without broad unicolorous patches of black or yellow hairs, eyes non-globular, tergal margins slightly lightened hyaline, hind basitarsis with mixture of black hairs), a species known from the Eastern Himalayas including the neighboring Indian state of Assam (Lieftinck 1974). Consequently, we synonymize *Tetralonioidella meghalayensis* with *Habropoda radoszkowskii* syn. nov. Hopefully, further efforts at imaging type specimens held outside of their home countries by various institutions will help avoid similar issues in the future (Orr et al. 2020, Warrit et al. 2023).

Additionally, the taxonomy of the relatively closely related subfamily Anthophorinae is also in need of clarification. Per Orr et al. (2022), the genus *Varthemapistra* Engel, 2018 was synonymized with *Habrophorula* based on several lines of evidence. Tran et al. (2024) later reversed this decision based on no additional data and the incorrect assertion that the “simple mandible” of the single described female representing *Varthemapistra* is unique (autapomorphic) among anthophorines, despite the fact that the genus is only documented from one sex and that females of *Anthophora peritomae* Cockerell, 1905 also have simple mandibles (noted in Orr et al. 2022, but not mentioned by Tran et al. 2024). To avoid moving *A. peritomae* to a monotypic genus on the other side of the world based on a single character (as the other defining characters of *Varthemapistra* are neither unique nor compelling, including even the color of the metatibial pubescence), and to avoid over-complicating the taxonomy of a region most needing of taxonomic stability (Warrit et al. 2023), we continue to follow the conclusions of Orr et al. (2022), treating *Varthemapistra* as a junior synonym of *Habrophorula*. We further hope that taxonomists working in these and other groups can, going forward, focus on stability and make only necessary change rather than promulgating unnecessary new higher-level names for single species.

Mimicry

The three-tiered mimicry systems described here raise several interesting new questions that require further investigation. First and foremost, are the selective pressures that resulted in brood parasitic mimics being exerted by predators, or by the hosts themselves? The case for predation driving mimicry has long been established, but it may be initially unclear how hosts could also select for color patterns. In the case of Anthophorinae, they are highly visual bees known to actively come and visually inspect people in the field (Thorp 1969). When encountering brood parasites and other nest invaders, violent

reactions have been documented in multiple instances for numerous species, including actively chasing various flies and brood parasitic bees away from nest sites (Thorp 1969; Batra 1978; Orr et al. 2016). By appearing similar to their hosts, brood parasites might be able to avoid these defensive behaviors when attempting to invade the nests of *Anthophora* and relatives; this would be especially useful at large aggregations, where numerous active females could inadvertently protect other nests by chasing brood parasites away from their own. Another potential example of at least host and brood parasite mimicking each other includes some South American brood parasites of *Epiclopus* Spinola, 1851 (Vivallo 2014) and their potential host *Centris cineraria* Smith, 1854, which also belongs to a group with high visual acuity (notably, the color pattern is also exhibited by some nearby members of *Alloscirtetica* Holmberg, 1903, *Megachile saulcyi* Guérin-Méneville, 1845, and *Svastrides* Michener, LaBerge, & Moure, 1955; it is also a rather simpler color form that might arise more easily by chance). The model in this example remains unclear, however, as suitable *Bombus* color patterns do not overlap, at least not with the range of *Epiclopus*. In contrast, the solitary bees *Andrena* (Andrenidae) are generally considered to rely less on vision when foraging, likely requiring less intense visual capability compared to fast-flying species. Their principal brood parasites in the genus *Nomada* (Apidae: Nomadinae) show no form of color similarity to them, and indeed *Nomada* may be under selective pressure to chemically mimic *Andrena* species instead (Tengö and Bergstrom 1977), or there may be less pressure since many *Andrena* do not or weakly sting, though evidence for this conjecture overall is extremely limited. Experimental manipulations including color alteration of brood parasitic bees could prove useful for testing whether hosts in these systems might be exerting selective pressures leading to mimicry as a means to escape them (although some interactions are limited to the confines of dark nests where visual features would be less useful).

Of interest is also that all confirmed melectine mimics fall within *Tetralonioidella*. Though almost all melectine bees are associated strictly with Anthophorinae, and therefore, they might benefit from resembling their often violent hosts as described above, no other melectine species conclusively exhibit such coloration. However, Lieftinck (1972: 301) mentions remarks by Popov (1955), who associated *M. (Paracrocisa) kuschakewiczi* (Radoszkowski, 1890) with “*Anthophora semperi* Morawitz” the latter being a large, black bee with white spots on the metasoma. However, *A. semperi* Morawitz does not exist, and should rightfully be *A. semperi* Fedtschenko, 1875 which may be a junior synonym of *A. dubia* Eversmann, 1852 depending on the identity of the type material of *A. dubia*, which is currently unavailable for study. In any case, given the abundance of black and white color patterns in melectines, it remains unclear whether any association is biologically meaningful; there are no black and white-spotted anthophorine hosts in most of the Old-World Mediterranean basin, where black-and-white melectines are diversified. It is, therefore, possible that some other melectine genera mimic their anthophorine hosts, but this should be conclusively established with new studies. Notably, *Melecta* and other melectine genera in Asia can be found in proximity with many bumble bee species but do not mimic them, so we would suggest that proximity alone does not make mimicry inevitable. It may simply be that the unusual hairiness of many of the *Tetraloni-*

oidella, in comparison to nearly all other Melectini, made them pre-adapted to the use of color for mimicry of bumble bees, as most bumble bees also have at least medium-length hairs. *Eupavlovskia* is an exception, also with much longer and denser hair on the mesoscutum, but predation pressures may simply vary by region, their genomic architecture may not include the type of variation necessary, and it has not mutated sufficiently, or the evolutionary chance of engaging in mimicry has simply not occurred.

The habitats of the brood parasites, their hosts, and likely *Bombus* models generally seem to align, especially given that most have been collected together, but this may be due to limited distributional records and collecting effort. The distribution of *Tetralonioidella mimetica*, its likely host, and potential *Bombus* models are interesting from the perspective of color pattern matching. The new species *T. mimetica* differs slightly from its likely host (*H. mimetica*) in that the former does not have the transverse black scutum hair stripe of the latter, nor does it have yellow hair on any of the first several terga (Fig. 5). Conversely, *H. mimetica* and *T. tricolor* more closely align with group 133 (Williams 2007), which are more common and species-rich in the region and overall compared to other groups (Williams et al. 2009). Instead, the best match for *T. mimetica* is group 134 of Williams (2007), which is unexpectedly most species-rich and abundant in the Transhimalaya of Ladakh and Zaskar and adjacent westward areas, from which *T. mimetica* is currently not known. In Sichuan, where *T. mimetica* appears most common, *Bombus* with similar color patterns are still found, but they are rare and generally at higher elevations (Williams et al. 2009). One possible explanation is that *T. mimetica* is present in the western Himalaya but has yet to be documented there, which seems feasible considering the rarity of the species and the considerable distribution of the related *T. himalayana* (from the eastern Himalayan to Taiwan, although it appears disjunct). It is also possible that they co-occurred in the past, as distributions are likely to have changed with climatic shifts. In the absence of this potential larger distribution, it is not immediately clear why it does not more closely match local model species (or its host). It may simply be that this is a case of imperfect mimicry, such that benefits are had without too closely matching a given model (Kikuchi and Pfennig 2013).

The interplay of various factors on the quality of mimicry is also a topic worthy of further consideration, as it could help to explain distributional mismatches or some cases of imperfect mimicry. *Tetralonioidella* are generally medium-sized bees, so under the theory that larger prey animals must better resemble the protected species they imitate (Penney et al. 2012), we would expect them to show close matching to their models. The black line of hairs on the scutum seen in *T. tricolor* but not in *T. mimetica*, which is also seen or not in some bumble bees, may also have physiological effects of helping to dissipate heat (Williams 1991; Williams 2007). These types of systems, especially bumble bees with their high intraspecific variation, offer an interesting natural lab for testing the various potential trade-offs involved in mimicry, and could prove increasingly useful to study as ongoing climatic changes might amplify the influence of physiological considerations in such systems.

The bees of Asia present a unique and interesting opportunity for the further exploration of mimicry in bees. For example, the carpenter bees of the subgenus *Bombioxylocopa*

Maa, 1939 all appear to be mimics, and numerous other species have epithets referring to their color patterns resembling bumble bees, such as *Amegilla bombiomorpha* Wu, 1983 (similar to *T. tricolor*). However, questions remain as to whether some color forms indicate mimicry or simple aposematism. For instance, there are many Hymenoptera and other insects (potential mimics) that exhibit an all-black form with a red tail, which for aculeate Hymenoptera would clearly indicate the location of the sting. Simple color forms such as this are considerably more difficult to link to mimicry than are the more complex types exhibited by bees such as *T. mimetica*, given the number of coordinated changes necessary for the latter to evolve, and more work is clearly necessary to further explore these phenomena.

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Supplementary material 1

Supplemental text and details

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Data type: docx

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Supplementary material 2

RaxML tree file

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Data type: barcodes_constrained

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